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On the exponent in the von Bertalanffy growth model

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Bertalanffy proposed the differential equation \( m'(t) = p \times m(t)^a - q \times m(t) \) for the description of the mass growth of animals as a function \( m(t) \) of time \( t \). He suggested that the solution using the metabolic scaling exponent \( a = 2/3 \) (von Bertalanffy growth function VBGF) would be universal for vertebrates. Several authors questioned universality, as for certain species other models would provide a better fit. This paper reconsiders this question. Using the Akaike information criterion it proposes a testable definition of ‘weak universality’ for a taxonomic group of species. (It roughly means that a model has an acceptable fit to most data sets of that group.) This definition was applied to 60 data sets from literature (37 about fish and 23 about non-fish species) and for each dataset an optimal metabolic scaling exponent \( 0 \leq a_{opt} < 1 \) was identified, where the model function \( m(t) \) achieved the best fit to the data. Although in general this optimal exponent differed widely from \( a = 2/3 \) of the VBGF, the VBGF was weakly universal for fish, but not for non-fish. This observation supported the conjecture that the pattern of growth for fish may be distinct. The paper discusses this conjecture.
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Abstract. Bertalanffy proposed the differential equation \( m'(t) = p \cdot m(t)^a - q \cdot m(t)^b \) for the description of the mass growth of animals as a function \( m(t) \) of time \( t \). He suggested that the solution using the metabolic scaling exponent \( a = 2/3 \) (von Bertalanffy growth function VBGF) would be universal for vertebrates. Several authors questioned universality, as for certain species other models would provide a better fit. This paper reconsiders this question. Using the Akaike information criterion it proposes a testable definition of ‘weak universality’ for a taxonomic group of species. (It roughly means that a model has an acceptable fit to most data sets of that group.) This definition was applied to 60 data sets from literature (37 about fish and 23 about non-fish species) and for each dataset an optimal metabolic scaling exponent \( 0 \leq a_{opt} < 1 \) was identified, where the model function \( m(t) \) achieved the best fit to the data. Although in general this optimal exponent differed widely from \( a = 2/3 \) of the VBGF, the VBGF was weakly universal for fish, but not for non-fish. This observation supported the conjecture that the pattern of growth for fish may be distinct. The paper discusses this conjecture.

Keywords: Akaike’s information criteria (AIC), multi-model inference, von Bertalanffy growth function (VBGF), metabolic scaling exponent, weak universality

1. Introduction

Growth models: Size at age is a key metric of productivity for any animal population (MacNeil et al., 2017) and since Verhulst’ (1838) seminal work about the logistic function a wide range of growth models to describe the size of animals as a function of time has been developed. Amongst applications are improved otolith analysis for age estimation (Ashworth et al., 2017, based on Vigliola and Meekan, 2009) or stock assessments in fisheries management (Juan-Jorda et al., 2015). The resulting information about life history and population structure has been applied e.g. in ecology, where the age structure of coral reef destructing starfish populations was reconstructed from size measurements and used to explain outbreaks (Pratchett, 2005).

Of particular interest are models based on biological principles. One class of such models was developed by Bertalanffy (1957) and Pütter (1920), who formulated a differential equation of ontogenetic growth (assuming \( 0 \leq a < b \); this paper assumes in addition \( b = 1 \)):

\[
(1) \quad \frac{dm(t)}{dt} = p \cdot m(t)^a - q \cdot m(t)^b
\]

Equation (1) aims at explaining the allocation of metabolic energy between growth and sustenance of an organism: If \( m = m(t) \) is body mass (weight) at age \( t \), then the body utilizes resources at a metabolic rate \( (p \cdot m^a) \) for growth, except for the resources allocated to the operation and maintenance of existing tissue \( (q \cdot m^b) \). The parameters \( p \) and \( q \) are positive scaling constants obtained by fitting the model curve (1) to growth data. Growth functions described by equation (1)
with $a > 0$, $q > 0$ are bounded and of a sigmoid shape with an asymptotic weight limit $m_{\text{max}} = (p/q)^{(1/(b-a))}$; the inflection point is assumed, when body mass reaches the fraction $(a/b)^{(1/(b-a))}$ of that weight limit (the right hand side of the differential equation and its derivative, respectively, vanish).

In general, the equation (1) can only be solved with elliptic functions (Ohnishi et al., 2014). Bertalanffy (1957) provided an explicit solution of equation (1) for exponents $0 \leq a < b = 1$ with elementary functions ($\exp =\text{exponential function}$): 

$$m(t) = \left( \frac{m(t)}{m_{\text{max}}} \right)^{1-a} = 1 - \left( 1 - \left( \frac{m_{0}}{m_{\text{max}}} \right)^{1-a} \right) \cdot \exp(-q \cdot (1-a) \cdot t)$$

Formula (2) explains growth in terms of the asymptotic weight limit (mature body mass) $m_{\text{max}}$ and the initial value (neonate weight) $m_{0} = m(0)$. This choice of parameters follows a recommendation of Cailliet et al. (2006). Richards (1959) provided another solution of (1) for $b > a = 1$ to model plant growth (e.g. Verhulst’s model: $a = 1$, $b = 2$).

**Is there a true exponent?** This paper asks, if the growth of different species needs to be modeled by different metabolic scaling exponents $a < 1$ in equation (2). The null hypothesis would state that on the contrary a certain universal metabolic exponent would suffice.

To resolve this question, the growth model (2) was applied to 60 data sets and best fit exponents $a_{\text{opt}}$ together with suitable parameters $m_{0}$, $m_{\text{max}}$ and $q$ were determined, using nonlinear regression by means of the method of least squares. As is illustrated by Figure 1, for certain data sets the choice of the optimal exponent resulted in a clear improvement of the fit.

**INSERT Figure 1**: Comparing the fit of model (2) with different exponents to growth data.

Several concrete values of the metabolic scaling exponent for the model (2) have been discussed in literature and the question, if the true exponent would be $a = 2/3$ or $a = \frac{3}{4}$ has been a topic of scientific controversy (Isaac and Carbone, 2010).

Bertalanffy (1934, 1949, 1957) suggested that model (2) with $a = 2/3$ would describe the growth of vertebrates; this defines the classical von Bertalanffy growth function (VBGF). Bertalanffy derived it from equation (1) by the following reasoning: Anabolism (synthesis for growth) would be proportional to the $2/3$ power of body weight ($a = 2/3$), as the oxygen consumption would be proportional to surface ($2/3$ power of volume), whereas catabolism (energy use for the maintenance of biomass) would be proportional to body weight ($b = 1$). This choice of exponents was supported e.g. by Banavar et al. (2002) and White and Seymour (2003).

Bertalanffy identified also species, where growth would be better described by model (2) with an exponent $a = 0$. This is the model of bounded exponential growth, where $m_{\text{max}} - m(t)$ is described by the model of exponential decay. Further, Bertalanffy observed that if mass growth is described by the VBGF and if mass is assumed to be proportional to the third power of length, then the growth of length is modeled by bounded exponential growth. And conversely, if length grows according to the bounded exponential growth model, then mass growth is described by the VBFG.

In this sense these two models are equivalent and in literature both models are referred to as VBGF. (For this paper, VBGF is defined by the exponent $a = 2/3 \approx 0.67$.)
West et al. (2001) proposed an alternative to the VBGF. They argued, that growth would better be described by the model function (2) with exponent \( a = \frac{3}{4} \), as the number of capillaries would be proportional to the \( \frac{3}{4} \)th power of the number of cells. This model was supported by Darveau et al. (2002). A metabolic exponent \( a = \frac{3}{4} \) had been suggested already earlier by Kleiber (1947).

However, more recent literature observed that no single metabolic exponent may be exactly correct and that perhaps the exponent may be unrelated to metabolism. (Noisy data may hide it; c.f. Batt and Carpenter, 2012.) As Killen et al. (2010) and White (2010) observed, for different species there were different optimal exponents \( a_{opt} \). Also for the same species different data sets supported different exponents. Amongst the stated reasons were environmental factors (e.g. food composition, temperature); c.f. Kimura (2008), Porch (2002), Quince et al. (2008), Stewart et al. (2013), or Yamamoto and Kao (2012). Further, asking for exponents that would be characteristic for a species may be ill-posed. For, due to random fluctuations one can expect that the best fit exponents for different samples for the same species might not be exactly the same. As Shi et al. (2015) observed, for some data sets a near-optimal fit could be achieved by a wide range of exponents, whence such fluctuations might lead to the identification of widely different optimal exponents.

**INSERT Figure 2**: Akaike weights for different exponents, when compared to the optimal exponent

Thus, the identification of an optimal exponent alone may be misleading, if there is no additional information about the achieved goodness of fit to the data. This paper applies Akaike’s information criterion (more specifically the Akaike weight) for this purpose. Given an optimal exponent \( a_{opt} \) computed for a certain data set and a hypothesized universal exponent \( a_{univ} \), the Akaike weight \( \text{prob}(a_{univ}) \) is the probability that the model (2) using the universal exponent \( a_{univ} \) is true, when compared with the optimal exponent \( a_{opt} \). Figure 2 displays the Akaike weights for a certain dataset.

**Problem of the paper**: Summarizing, the above informal question may be recast into the following testable form. Given a data set, a metabolic exponent \( 0 \leq a < 1 \) is refuted for this data set, if in comparison to the optimal exponent for model function (2) its Akaike weight is below 2.5%. Given a taxonomic group of species (e.g. ‘all fish’), then an exponent is weakly universal for this group, if with 90% confidence at least 90% of randomly chosen data sets from this group do not refute that exponent.

Variants of the definition of ‘weak universality’ can be obtained with different thresholds; the present percentages were used for the proof of principle, only. The notion of refutation remains meaningful, if the Akaike weight is merely used as an index for the goodness of fit, as in that case ‘below 2.5%’ defines the 5% of the index values with the worst fit. Further, the use of confidence limits in the definition leaves room for alternative models for exceptional species and it acknowledges that certain data sets may not be appropriate for further analysis by growth models of type (2), whence such exceptional data sets should not refute a universal exponent. In view of the unknown distributions, this paper uses Clopper-Pearson confidence limits (Casella and Berger, 2001), which are conservative (higher confidence, than nominally stated) and also suitable for
small sample sizes (as for the proof of principle small samples suffice, whereby a sample consists of different data sets).

Of particular interest is the question, if the exponent $a = 0.67$ of the VBGF is weakly universal for fish. For, the VBGF is widely used to describe the growth of fish and many authors reported an excellent fit (e.g. Koch et al., 2015). For instance, the FishBase database (Frose and Pauly, 2017) presumes VBFG and lists growth parameters for 2320 species. A search in Google Scholar (August 2018: combining with AND the key phrases Bertalanffy, ‘growth model’, ‘fish growth’) identified approximately 24,800 papers. Smart et al. (2016) surveyed the literature about growth of elasmobranch species (e.g. sharks) and the VBGF (with or without prescribing an initial value for size at $t = 0$) was studied twice as often as any other model.

2. Materials and methods

Choice of the growth model: Model (2) has been chosen for this study, as its metabolic scaling exponent is believed to have a biological meaning. This distinguishes it from simpler models recommended in literature for data interpolation, such as power-laws between size and age (Katsanevakis and Maravelias, 2008).

Another feature is the sigmoid shape: For model (2) with exponent $a > 0$ the rate of mass growth increases, as size increases, until it reaches a maximal rate (inflection point) and then decreases towards zero as mass approaches the asymptotic weight limit $m_{\text{max}}$. Whether the growth data show a sigmoid shape can be verified graphically by a Walford plot (Figure 3) of growth rate over size (unimodal curve, peaking above the weight at the inception point).

Further, despite its dependency on merely three parameters plus the metabolic exponent, model (2) is flexible enough to represent growth curves of different sigmoid shapes and it is amenable to data fitting by means of spreadsheets. Spreadsheets may be used also for more complex models, if numerical solutions of differential equations (e.g. Leader, 2004) are used, but then numerical errors would require further analysis.

In literature there are different parametrizations of model (2). In relation to the parameters of equation (1), assuming $b = 1$ and using the formula for $m_{\text{max}}$, $p = q \cdot m_{\text{max}}^{1-a}$. The constant in the exponent of (2), $q \cdot (1-\alpha)$, corresponds to the ‘growth coefficient’ $k$. Further, several papers used a time shift $t_0$ to eliminate the multiplicative constant in (2). However, $t_0$ might not have a biological meaning (Schnute and Fournier, 1980). The main difference between the model curves (2) for different exponents was the weight at the inflection point, varying between 0% and 37% of $m_{\text{max}}$ (limits of $a^{1/(1-a)}$ for exponents $a \rightarrow 0$ and $a \rightarrow 1$).

Data sources: The authors considered only age-mass or age-length (for most fish) data. The main sources were Parks (1982), Ogle (2017) and the supporting information of West et al. (2001). The authors supplemented them by data from other literature sources or from data obtained by personal communications. Data in diagrams were retrieved by means of digitalization (Digitize-It of Bormisoft®).
For easier identification, data sets were numbered as follows.

The original published sources of the data for fish were Cubillos et al. (2001) for #1 Anchoveta (Engraulis ringens), #2 Araucanian Herring (Strangomera bentincki) and #26 Sardine (Strangomera bentincki); Jørgensen (1992) for #3 Atlantic (Arctic) Cod (Gadus morhua); Maceina (2007) for #5 Blue Catfish (Ictalurus furcatus); Stewart et al. (2013) for #6-7 female and male Australian Bonito (Sarda australis); Abad (1982) for #9 Sea (Brown) Trout (Salmo trutta fario); Parker et al. (2007) for #10 Bull Trout (Salvelinus confluentis), whereby the authors removed an outlier; Mooij et al. (1999) for #13 European Perch (Perca fluviatilis); Brown and Rothery (1993) for #14 time-weight data of Guppy (Poecilia reticulate = Lebistes reticulatus in the source); Yildirim (2003) for #16 Jonubi (Chalcalburnus mossulensis); Jobes (1946) for the meanwhile extinct #20 Longjaw Cisco (Coregonus alpenae = Leucichthys alpenae in the source) at two locations; Vaughan & Helser (1990) for #21 Red Drum (Sciaenops ocellatus); Moreau (1979) for #22 Redbreast Tilapia (Coptodon rendalli = Tilapia rendalli in the source); Wolfert (1980) for #23 Rock Bass (Ambloplites rupestris); Bailey (1963) for #24 Round Whitefish (Prosopium cylindraceum); West et al. (2001) for #25 time-weight data of Sockeye Salmon (Oncorhynchus nerka); Grabowski et al. (2012) for #29 Spotted Sucker (Minytrema melanops); Krüger (1973) for #30 Atlantic Bluefin Tuna (Thunnus thynnus); House and Wells (1973) for #31 Troutperch (Percopsis onsicomaycus); Ianelli et al. (2011) for #33 Walleye Pollock (Theragra chalcogramma); Araujo and Martins (2007) for #34-35 female and male White Grunt (Haemulon plumieri); Gomez-Requeni et al. (2010) for #36 time-weight data of male Zebrafish (Danio rerio) and Kaushik et al. (2011) for #37 Zebrafish larvae.

Further fish data originated from other resources of Ogle (2017) for #4 female Black Drum (Pogonias cromis), #8 Sea (Brown) Trout (Salmo trutta) and Rainbow Trout (Oncorhynchus mykiss), #11 Cabezon (Scorpaenichthys marmoratus), #12 Atlantic Croaker (Micropogonias undulatus), #15 Jackass Morwong (Nemadactylus macropterus), #17 Lake Erie Walleye (Sander vitreus), #18-19 female and male Arctic Lake Trout (Salvelinus namaycush), #27-28 female and male Siscowet Lake Trout (Salvelinus namaycush), and #32 Virginia Spot (Leiostomus xanthurus).

The original published sources of the data for non-fish species were Brody (1945) for #38 Cattle (Bos primigenius taurus), #40 Chicken (Gallus gallus domesticus) and #57 Rat (Rattus rattus); Grossmann (1969) for #42 Rhode Island chicken, Ricard (1975) for #44-46 about chicken strains X33, X38 and X44; Elke Schläger (personal communication) for #47 Rhodesian Ridgeback dog (Canis lupus familiaris), Renner-Martin et al. (2016) for #50 Domestic Pig (Sus scrofa domestica); Sturm (2003) for Cricket larvae #51 (Acheta domestica), #52 ( Gryllus assimilis) and #53 (Teleogryllus commodus); Owen (1960) for #54 Heron (Ardea cinerea) and #58 Robin (Erithacus rubecula); Fabian Bader (personal communication) for #55 Ball Python (Python regius); Forsyth (1976) for #59 Shrew (Sorex cinereus); and Rudstam (1989) for #60 Shrimp (Mysis mixta).

Further non-fish data originated from unpublished resources of Parks (1982) for #39 Friesian cattle, #41 and #43 about Apollo and Ross Fryer chicken, #48-49 female and male Great Dane dogs, and #56 albino rats.
**Data selection and preprocessing:** Only data sets with \( N = 6 \) or more points of time were considered, regardless of how many animal observations were available for each point of time. Amongst data sets removed for this reason were Channel Darter (*Percina copelandi*) and Creek Chub (*Semotilus atromaculatus*) from Ogle (2017) based on Reid (2004) and Quist et al. (2012). For non-fish species, the authors did not consider (hunting or capturing) data of wildlife (e.g. Read et al., 1993, for Bottlenose Dolphin; Pei, 1996, for Muntjak Deer; or Smuts, 1975, for Burchell’s Zebra), where animal age was estimated. However, for fish, data sets using age estimates were not removed. Consequently, for fish spawning time caused age uncertainties (Datta and Blanchard, 2016).

In order to use data of the same format, data were transformed into mean-weight-at-time data. Most data for non-fish species were of this form. For fish, most data were about length. Empirical evidence suggested that for fish mass may be related to length by an allometric power relation \( m(t) = c \cdot l(t)^p \) with \( 2.5 < p < 3.5 \) and some constant \( c \) (Pauly, 1979; Anderson and Neumann, 1996). The paper approximated mass for all time-length data by the third power of length. This convention was in line with Bertalanffy (1934, 1957) and it avoid mixing up information from different sources about time-length and length-mass relations. The direct comparison of length data between e.g. fish and birds was avoided, as ‘length’ was ambiguous (e.g. Holden and Raid, 1974: standard length, fork length, total length).

Further, the search for data was confined to data of the growth from an early point in life (birth) till the end of the growth phase (e.g. sexual maturation). For otherwise, as is illustrated by Figure 4, a data set might not capture the full phase of growth, and the modeling of a growth curve would depend on extrapolation. This has been an issue for one data set (Figure 5).

**Statistical methods:** Generally, computations were done in Microsoft® EXCEL. Casella and Berger (2001) was used as a standard reference for statistics and XL-Stat of Addinsoft® for statistical computations.

For Clopper-Pearson confidence limits, given a sample of size \( M \) (here the number of data sets) and amongst them \( m \) ones with a specific property (here the number of data sets not rejecting a certain exponent), then using the beta distribution and EXCEL notation, the one-sided lower 90%-confidence limit and the upper 90%-confidence limit for the frequency of this property in the population were \( 1 - \text{BETA.INV}(0.9; M-m+1; m) \) and \( \text{BETA.INV}(0.9; m+1; M-m) \).

**Data fitting:** The paper used nonlinear regression by means of the method of least squares. Given an exponent in \( 0 \leq a < 1 \), optimal parameter values \( m_0, m_{max}, \) and \( q > 0 \) for model (2) were sought to minimize the sum of squared residuals, \( \text{SSR} \), between the data points and the model function. (Recall that the squared residual for the \( n \)th data point \((t_n, m_n)\) is \((m_n - m(t_n))^2\).) Optimization used the SOLVER Add-In of Microsoft EXCEL, which implemented an iterative optimization method (Newton’s method).
Next, the paper sought to obtain an optimal exponent, where \(SSR = SSR(a)\) was minimal; the desired accuracy for the exponent was 1/100. Therefore, using a macro the optimization was repeated for each exponent \(a = 0, 1/100, 2/100, \ldots \ 99/100\) and the resulting minimal values of \(SSR(a)\) were tabulated. Summarizing, this defined an optimal exponent \(a_{opt} < 1\) and optimal parameter values \(m_0, m_{\text{max}}, \text{and } q\) for this exponent.

**INSERT Figure 6**: Transformation of time-mass-data and a regression line for the transformed data set

A disadvantage of the present method, when applied to the considered data, was numerical instability. Therefore, optimization was done in two steps, whereby in the first step good initial estimates of the optimum parameters were computed by adapting a graphical method (Figure 6), the Bertalanffy-Beverton plot (Bertalanffy, 1934). It aims at an optimal fit of the weight-time data to the inverse function of (2), described by equation (3) for \(t = t(m)\); \(\ln\) is the natural logarithm function:

\[
(3) \ t = \frac{f(m_0) - f(m)}{q} \quad \text{where } f(x) = \frac{\ln(1 - (x/m_{\text{max}})^{1+a})}{1-a} \quad \text{for } x > m_{\text{max}}
\]

Collecting terms not depending on \(m\), this is simplified to equation (4):

\[
(4) \ t = A + B \cdot f(m) \quad \text{with } A = f(m_0)/q, \ B = -1/q
\]

Assuming a given exponent and a given asymptotic weight limit \(m_{\text{max}}\), a linear regression line \(t = A + B \cdot u\) was fitted to transformed data \((u_n, t_n) = (f(m_n), t_n)\), using the function \(f\) of equation (3) and computing \(A\) and \(B\) with the LINEST function of EXCEL (Figure 6). Its goodness of fit was evaluated by the sum of squared residuals \(SSR_{\text{inv}}(m_{\text{max}})\); it was dependent on \(m_{\text{max}}\).

Next, the exponent was kept fixed and \(m_{\text{max}}\) was allowed to vary: The function \(SSR_{\text{inv}}(m_{\text{max}})\) decreased rapidly for \(m_{\text{max}}\) near the observed maximum and was flat for larger values of \(m_{\text{max}}\) (Figure 7). The SOLVER Add-In minimized this function iteratively (a starting value 1% above the observed maximum weight was chosen). As the optimization used exact formulae for \(A\), \(B\) and was done in one dimension (seeking \(m_{\text{max}}\) with minimal \(SSR_{\text{inv}}\)), it could be performed fast and with high precision.

For a given exponent, this optimization defined \(m_{\text{max}}, A\) and \(B\), from which \(q = -1/B\) and \(m_0 = m_{\text{max}} \cdot (\exp(A \cdot (a-1)/B) - 1)^{1/(1-a)}\) were computed.

These values were used as starting values for the second step, the iterative optimization of \(SSR\). Given an exponent \(a\) and starting with the above parameter values \(m_0, m_{\text{max}}, \text{and } q\), these values were successively improved to compute the minimal \(SSR(a)\).

**INSERT Figure 7**: Optimizing the asymptotic weight limit (fit to weight-time data)

The two optimization steps compare as follows: The second step assumed that age was controlled and that the weight observations came from a random sample of animals with a given age; this was the traditional approach towards nonlinear regression. The first step assumed that age was random for a given weight. Piner et al. (2012) compared these methods and recommended the first step as a viable alternative to the traditional approach. Also Sparre and Venema (1988) suggested this method. However, this paper used the traditional approach, as all non-fish data were controlled.
for age. As for a computationally simpler method, there is a large body of literature using the Walford plot for data fitting (e.g. Espino-Barr et al., 2015), which was explained in Figures 3 and 5. However, that method did not always provide good initial estimates.

In order to retain \( m_{\text{max}} \) as an asymptotic limit (and as otherwise the transformed data would not be defined), the constraint that \( m_{\text{max}} \) should exceed the maximal observed mass was added. As for some data sets the optimal \( m_{\text{max}} \) was extremely high without substantially improving on \( \text{SSR}_{\text{inv}} \), another constraint was added, that \( m_{\text{max}} \) should not exceed hundred times the maximal observed mass.

**Model comparison:** In order to compare the goodness of fit, for each data set the 100 models corresponding to different exponents \( a < 1 \) were assessed by means of the Akaike information criterion (Akaike, 1974; Burnham and Anderson, 2002; Motulsky and Christopoulos, 2003), using an index \( AIC_c \) for small sample sizes. It was computed from \( \text{SSR}(a) = \text{the sum of squared residuals} \), \( N = \text{number of data points} \), and \( K = 4 = \text{number of optimized parameters (namely } m_0, m_{\text{max}}, q \text{ and implicitly } \text{SSR}) \). The number of data points essentially counted, for how many points of time there were data. (If there were several observations for the same point of time, as e.g. for reported average values, then this was counted as one data point.)

\[
(5) \quad AIC(a) = N \cdot \ln \left( \frac{\text{SSR}(a)}{N} \right) + 2 \cdot K + \frac{K \cdot (K + 1)}{N - K - 1}
\]

\[
(6) \quad \text{prob}(a) = \frac{e^{-\Delta/2}}{1 + e^{-\Delta/2}}, \text{where } \Delta = AIC(a) - AIC(a_{\text{opt}}) > 0
\]

Formula (6) gives the probability \( \text{prob} \) (Akaike weight: see Figure 2) that the model with exponent \( a \) was true, when compared with the better fitting model with exponent \( a_{\text{opt}} \), assuming that either \( a \) or \( a_{\text{opt}} \) would be the true exponent. However, neither exponent may be true and the paper makes no assumption thereabout, as this is not needed for the criterion of refutation: If a model (defined from an exponent \( a \)) is refuted, as it fares poorly amongst its ‘peers’, it is sensible to refute it also for any larger group of models.

**Data quality:** Data quality is an elusive concept. This paper quantified it by the indicator FNR, the fraction of non-refuted exponents for model (2). Recall that that 100 exponents \( a = 0, 0.1, \ldots, 0.99 \) were compared and that an exponent was refuted, if \( \text{prob}(a) < 2.5\% \). If High and Low were the highest and lowest non-refuted exponents (c.f. Tables 1 and 2 below), then FNR was the difference between High and Low plus 0.01.

This definition will be justified below by a discussion of certain issues about data quality, which translated into longer intervals of non-refuted exponents.

### 3. Results

Tables 1 and 2 summarize the fit of model (2) to the 60 fish and non-fish data and Figure 8 plots, for each exponent, confidence intervals for the percentages of non-rejection.

**INSERT Table 1.** Optimal exponents and interval of non-refuted exponents for fish data

**INSERT Table 2.** Optimal exponents and interval of non-refuted exponents for non-fish data
Contrary to the assumption that the metabolic exponent may be characteristic for a species, the best fitting metabolic exponents could differ widely for female and male fish of the same species. (For F and M of Lake Trout in #18-19 of Table 1 the best exponents were 0.69 and 0.28, respectively.) The concept of non-rejection relativized these differences. For, amongst the considered data sets the non-rejection intervals of female and male animals of the same species were overlapping, allowing for the selection of a common exponent suitable for both sexes.

Figure 8 generalized this reasoning by counting, for each exponent $0 \leq a < 1$, for how many fish data sets (as percentage) this exponent was not rejected. (Thus, it was counted, for how many lines of Table 1 the exponent was between Low and High.) There was a first peak for exponents 0.66 and 0.67, which were not rejected for 36 data sets (97% of 37 data sets). Further, exponents $a \geq 0.9$ were not rejected for 97% of the data sets. Under the assumption, that the data sets and species were selected at random from the universe of all fish data sets, statistical reasoning could be applied: For these peak exponents the lower one-sided Clopper-Pearson confidence limit (90% confidence) was 90%. Specifically, with 90% confidence the VBGF (exponent $a = 0.67$) should not be rejected by at least 90% of fish data sets.

Hence, based on the present data set, it could be concluded that the VBGF was weakly universal for fish.

Notably, for the exponent $a = 0.75$ proposed by West et al. (2001) weak universality for fish could not be established. For the non-fish data, no weakly universal exponent could be identified. Both observation may be explained by the too low number of data sets (resulting in broader confidence intervals).

Considering the upper one-sided confidence limits (90% confidence) for the fish data, for exponents $a \leq 0.5$ these were below 89%, whence such exponents might not be weakly universal for fish. For non-fish data the upper confidence limit was below 89% for exponents $a \leq 0.88$ whence the VBGF ($a = 0.67$), and more generally any exponent $a \leq 0.88$, might not be weakly universal for non-fish species.

**4. Discussion and conclusion**

**Do fish grow differently from non-fish species?** As noted above, the universality of the VBGF seems to distinguish fish from non-fish species. The authors therefore hypothesized that the pattern of mass growth may differ between fish and non-fish species.

An analysis of the optimal exponents ($a_{opt}$) provided support for this hypothesis. As the distribution of optimal exponents was unknown, a non-parametric location test was applied (Mann-Whitney test: computations in XL-Stat); it indicated with 95% significance ($p$-value 4.7%) that the mean value of the optimal exponents for fish (0.61) was stochastically lower than the mean value for non-fish (0.79). Further, Table 3 displayed a 99.99% significant contingency for the fit of the VBGF on the taxonomic group (fish or non-fish species).
Review of the data: The unusual high significance for an ambitious hypothesis not yet found in literature led to the question, if there was some non-biological peculiarity of the fish data that made the refutation of the VBGF more difficult for fish.

An obvious difference between fish and non-fish data was the transformation of length to weight, which was needed for most fish. This paper used a power-law transformation $m(t) = l(t)^p$ with $p = 3$ for fish. As Figure 9 illustrates, this convention could have affected refutations, but it could not explain a systematic bias towards easier or more difficult refutations. (In the figure, higher/lower values of $p$ make refutations easier/more difficult. However, for some data, the ‘true’ $p$ was below 3 and for others it was above 3.) Further, the VBGF was not rejected for the three time-weight fish data sets (#14 Guppy, #25 Salmon, and #36 Zebrafish).

INSERT Figure 9: Effect on the Akaike weights of using different length-mass relations

INSERT Figure 10: Effect of outliers on the Akaike weights

Data with outliers are obviously of poor data quality. For such data, the refutation of exponents turned out to be more difficult, i.e. FNR became larger; Figure 10 illustrates this. Therefore, in order to remove non-refutations caused by poor data quality, obvious outliers had to be removed. (The authors removed an outlier from a data set.)

Further, while for non-fish species the data for females and males of the same species were collected separately, this was not the case for all fish. In case that these groups had a different growth pattern (different optimal exponents), the combination of data could result in higher residuals, making refutations more difficult and increasing FNR (Figure 11). This effect was particularly extremal for the Black Drum (*Pogonias cromis*) data from Ogle (2017), where the combined data did not allow to refute any exponent and also the sigmoid growth pattern was lost (optimal exponent $a = 0$ for the combined data), whereas the Akaike weights for females showed a clear peak. (The Akaike weights for males were not meaningful by lack of data.) The phenomenon of sex change was not considered, but literature did not report problems for the fit of a VBGF (c.f. Taylor and Pardee, 2017).

INSERT Figure 11: Effect of combining males and females on the Akaike weights

Where fish came from different locations (e.g. different water temperatures for the Lake Trout data #18-19 and #27-28), a different pattern of growth was expected for biological reasons. However, for other data, e.g. of Longjaw Cisco (*Coregonus alpenae*) from Ogle (2017) and Jobes (1946), the combination of data from two locations of the same lake did not seem to have notable effects (the paper used the combined data).

Another difference was related to how data were gathered: Data were either growth data for individual animals or average values. In the latter case, either the same group of animals was observed over a certain time span (e.g. feeding experiments), or completely different animals were observed (e.g. hunting data; these displayed the largest variations). Most non-fish data were about pets, farmed animals or laboratory animals, whose age was known, whose food intake was controlled and where the animals could easily be grouped by objective factors (e.g. sex, strain).

For fish, comparable data were conceivable only for aquarium fish, such as Guppy or Zebrafish.
Implications about data quality: Summarizing, there were differences in the data quality between fish and non-fish data. Consequently, for the fish data refutations may have become more difficult (larger FNR) and this could have been the reason, why the VBGF was not refuted for most fish data. This is tested below.

With 99.99% significance (Mann-Whitney test: $p$-value below 0.01%, computed in XL-Stat) the average FNR for fish (0.8) was stochastically larger than the average FNR for non-fish (0.38). Thereby FNR = 1 for 18 data sets, 17 of them for fish. Thus, apparently the larger FNR for fish was the reason for the high level of non-refutation of the VBGF for fish and the contingency in Table 3. However, there were also fish with good data quality in this sense; thus for Artic Cod (#3 in Table 1) a minimal FNR = 0.1 was observed.

The indicator FNR may also explain the different location of the optimal exponents for fish and non-fish, as with 99.99% significance the optimal exponents ($a_{opt}$) were negatively correlated with FNR (t-test: $p$-value below 0.01%, computed in XL-Stat). Thus, the lower optimal exponents for fish were related to a higher FNR.

Thereby, for 48% of the considered data sets it was conceivable that model (2) was not true, as the optimal exponent was found on the boundary of the considered domain. Thereby, for five data sets $a_{opt} = 0$ (indicating that growth was rather not sigmoid); these data sets were for fish and for them FNR = 1. For 24 of the 60 data sets (12 fish) the optimal exponent was maximal ($a_{opt} = 0.99$) and of them FNR = 1 for only four data sets (all fish).

Conclusion: The paper argued that the question, whether there exists a universal metabolic scaling exponent, may be ill-posed and it developed a mathematical definition of weak universality to reformulate this question in an empirically testable way. Applying this notion to 60 data sets about the growth of fish and non-fish species the data seemed to support the hypothesis that there would be a difference between fish and non-fish; for the former VBGF would be weakly universal. However, this ambitious hypothesis could not be maintained, as there were systematic differences between fish and non-fish in data quality, and these differences could have hindered the refutation of the VBGF for fish-data.

It may thus be concluded: The VBGF did adequately describe the growth of 97% of data sets for fish. Therefore, where the purpose of data fitting is the condensation of information to summarize growth data about wildlife by means of a few parameters, then the VBGF appears to be adequate. However, the reason for its adequacy may not be the ‘inherent truth’ of the VBGF, but rather a not so good quality of wildlife data in general.

Acknowledgements

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References


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Figure 1

Comparing the fit of model (2) with different exponents to growth data

Figure generated in Microsoft EXCEL, based on (time-length) data of Arctic Cod (*Gadus morhua*) from Jørgensen (1992), approximating weight by length\(^3\) and determining the least squares fit to these data of model (2) with exponents \(a = 0.67\) (VBGF = dashed line) and \(a = 0.99\), the optimal exponent.
Figure 2

Akaike weights for different exponents, when compared to the optimal exponent

Graphical multi-model comparison, generated in Microsoft EXCEL, based on time-length data of Sea Trout (*Salmo trutta fario*) from Abad (1982), approximating weight by length^3. The Akaike weight $prob(a)$ for the generalized von Bertalanffy model with exponent $a$ was computed in comparison with the optimal exponent $a_{opt} = 0.66$. The figure highlights also the Akaike weight (50%) of the VBGF ($a = 0.67$). The comparison presumes, that one of the two exponents $a$ or $a_{opt}$ is true ($prob(a) + prob(a_{opt}) = 100\%$) and that $prob(a) \leq prob(a_{opt})$, whence $prob(a) \leq 50\%$. As is suggested from this figure, exponents $a < 0.5$ may be refuted. For, either model (2) is false and then all exponents refuted. Or the model is true. Then even under the assumption that one of the exponents $a < 0.5$ or $a_{opt} = 0.66$ would be true, the probability for the truth of any exponent $a < 0.5$ would be negligible.
Figure 3

Weight increase and its approximation by a VBGF

Modification of the Walford plot (Walford, 1946; other modifications: Ford, 1933; Gulland, 1964) generated in Microsoft EXCEL, based on (time-length) data of Bull Trout (*Salvelinus confluens*is) from Ogle (2017) and Parker et al. (2007) with $dm/dt$ computed from the data by numeric differentiation (quadratic interpolation to take care of unequal $dt$-interval length: Burden and Faires, 1993). The model curve is right hand side of (1), with $p$, $q$ obtained from a linear fit (LINEST function applied to $dm/dt$, $m^a$, $m^b$ with $a = 2/3$, $b = 1$).
Figure 4

Dependency of the optimal exponent on which phase of growth was observed

The figure illustrates a) the general form of VBGF showing a characteristic S-shape over its whole range; b) missing end-data, which suggest unbounded growth; and c) missing data at the beginning, which suggests exponential bounded growth (exponent $a = 0$).
Figure 5

Weight increase and approximation by a logistic model, i.e. (1) with $a = 1$, $b = 2$

Modified Walford plot generated in Microsoft EXCEL, based on (time-length) data of Freshwater Drum (*Aplodinotus grunniens*) from Ogle (2017) and Bur (1984), and model curve computed as in Figure3. This data set was removed, as no data point supported the estimation of $m_{max}$ (selection criterion from Knight, 1968).
Figure 6

Transformation of time-mass-data and a regression line for the transformed data set

Generalized Bertalanffy-Beverton plot generated in Microsoft EXCEL, based on (time-mass) data of male Zebrafish (*Danio rerio*) from Gomez-Requeni (2010), transforming the time-mass data \((t,m)\) into \((u,t) = (f(m),t)\) and fitting a regression line \(t = A + B \cdot u\) with \(A = 22.486\) and \(B = 3.438\) to the transformed data. The function \(f\) was defined in equation (3) using the exponent \(a = 0.67\) and assuming an asymptotic weight limit \(m_{\text{max}} = 345\text{mg}\). The transformation required \(m_{\text{max}}\) to exceed the maximal observed weight \((344.4\text{mg})\), as otherwise the transformation would not be defined for all data points.
Figure 7

Optimizing the asymptotic weight limit (fit to weight-time data)

Figure generated in Microsoft EXCEL, based on (time-mass) data of Guppy (*Poecilia reticulata*) from West et al. (2001), referring to Brown and Rothery (1993): 14 data points (average weights) from days 0 to 88 with a maximal observed weight of 0.145g. Assuming an exponent $a = 0.67$, the sum of squared residuals $SSR_{inv}$ was plotted in dependency on $m_{max}$. The minimum was attained for $m_{max} = 0.165g$, resulting in $q = 0.1$/day and $m_0 = 0.03g$. This was used as a starting value for the minimization of $SSR$ for the fit of function (2) to the time-weight data. The resulting optimal parameters (for $a = 0.67$) were $q = 0.139$/day, $m_0 = 0.002g$ and $m_{max} = 0.149g$. 
Figure 8

Confidence intervals for the percentage of fish data sets not rejecting an exponent

Figure generated in Microsoft EXCEL, counting the percentage of how many of the 37 fish data sets of Table 1 did not reject the exponent on the x-axis together with the upper and lower one-sided Clopper-Pearson confidence limits (90% significance). The lower limit mattered for the weak universality criterion.
Figure 9

Effect on the Akaike weights of using different length-mass relations

Figure generated in Microsoft EXCEL, based on time-length data of Araucanian Herring (*Strangomera bentincki*) from Ogle (2017) and Cubillos et al. (2001), using different powers of length to estimate mass.
Figure 10

Effect of outliers on the Akaike weights

Figure generated in Microsoft EXCEL, based on (time-length) data of Bull Trout (*Salvelinus confluentis*) from Ogle (2017) and Parker et al. (2007), whereby for the correction one outlier was removed from the data. Data from the Arctic Long Term Ecological Research, separated by sex and combined.
Figure 11

Effect of combining males and females on the Akaike weights

Figure generated in Microsoft EXCEL, based on time-length data of Lake Trout (*Salvelinus namaycush*) from Ogle (2017), based on data from the Arctic Long Term Ecological Research, separated by sex and combined.
**Table 1** (on next page)

Optimal exponents and interval of non-refuted exponents for fish data

Data sets abbreviated (details in the text); F and M denotes data for females and males; $a_{opt}$ = metabolic scaling exponent with the best fit of model (2) to the data; non-refutation defines the lower and upper bounds of the interval consisting of those of metabolic exponents that in comparison to $a_{opt}$ could not be refuted (Akaike weight 2.5% or higher).
Table 1. Optimal exponents and interval of non-refuted exponents for fish data

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Notes: Data sets abbreviated (details in the text); F and M denotes data for females and males; $a_{opt}$ = metabolic scaling exponent with the best fit of model (2) to the data; non-refutation defines the lower and upper bounds of the interval consisting of those of metabolic exponents that in comparison to $a_{opt}$ could not be refuted (Akaike weight 2.5% or higher).
Table 2 (on next page)

Optimal exponents and interval of non-refuted exponents for non-fish data

Explanations as for Table 1.
Table 2. Optimal exponents and interval of non-refuted exponents for non-fish data

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<td></td>
<td>0.99</td>
<td>0.99</td>
</tr>
<tr>
<td>48</td>
<td>Dogs</td>
<td>0.84</td>
<td>0.99</td>
<td>60</td>
<td></td>
<td>0.99</td>
<td>0.99</td>
</tr>
<tr>
<td>49</td>
<td></td>
<td>0.99</td>
<td>0.99</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Explanations as for Table 1.
Table 3 (on next page)

Contingency of the rejection of the VBGF on the taxonomic group

The contingency table was based on the count of the number of rejections of the exponent $a = 0.67$ (VBGF). For all common tests (chi-squared, chi-squared with Yates continuity correction, Fisher exact test, simulation) the fish data of this paper differed from the non-fish data with 99.99% confidence ($p$-value below 0.01%). The odds ratio comparing the odds of non-rejection for fish with the odds for non-rejection of non-fish was $(36/1)/(8/15) = 67.5$ and its 95% confidence limits were 10.8 and 422.8. (The computations used XL-Stat.)
Table 3. Contingency of the rejection of the VBGF on the taxonomic group

<table>
<thead>
<tr>
<th>Number of data sets</th>
<th>Fish</th>
<th>Non-Fish</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>VBGF not rejected</td>
<td>36</td>
<td>8</td>
<td>44</td>
</tr>
<tr>
<td>VBGF rejected</td>
<td>1</td>
<td>15</td>
<td>16</td>
</tr>
<tr>
<td>Sum</td>
<td>37</td>
<td>23</td>
<td>60</td>
</tr>
</tbody>
</table>

Notes: The contingency table was based on the count of the number of rejections of the exponent $a = 0.67$ (VBGF).

For all common tests (chi-squared, chi-squared with Yates continuity correction, Fisher exact test, simulation) the fish data of this paper differed from the non-fish data with 99.99% confidence ($p$-value below 0.01%). The odds ratio comparing the odds of non-rejection for fish with the odds for non-rejection of non-fish was $(36/1)/(8/15) = 67.5$ and its 95% confidence limits were 10.8 and 422.8. (The computations used XL-Stat.)